
PALEOBOTANY, RELATIONSHIPS, AND GEOGRAPHIC HISTORY OF WINTERACEAE¹

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ABSTRACT

In combination with phylogenetic analyses of morphological and molecular data from modern plants, fossils allow improved reconstruction of the history of Winteraceae. Phylogenetic analyses link Winteraceae with Canellaceae, nested among Magnoliales, Laurales, and Piperales, implying that their lack of vessels is derived rather than primitive. The oldest records, from the Barremian and Aptian-Albian (Early Cretaceous) of Northern Gondwana (Gabon, Israel), are ulcerate tetrads (*Walkeripollis*) with an annulus underlain by thickened endexine but finer sculpture than modern Winteraceae, which most likely represent the stem-lineage leading to crown-group Winteraceae. Early Cretaceous *Afropollis* and *Schrankipollis*, which have also been compared with Winteraceae, are probably not related. The distribution of *Walkeripollis* implies that the winteraceous line originated in tropical, possibly dry, environments, like those of modern Canellaceae, rather than equable temperate and upland tropical habitats like those where Winteraceae occur today. Crown-group Winteraceae, first represented in the Santonian-Campanian (Late Cretaceous) by more coarsely reticulate tetrads in Australia and vesselless wood in Antarctica, and later by tetrads in South America and Africa, appear to be derived from a line that spread south into the temperate zone, consistent with ecological hypotheses that vessels were lost as an adaptation to cooler climates. Late Cretaceous paleogeography suggests that the crown-group could have dispersed to Australasia via either South America and Antarctica or Madagascar (where the family is represented by the basal genus *Takhtajania*) and India.

Key words: angiosperms, biogeography, Cretaceous, paleobotany, palynology, phylogeny, Tertiary, Winteraceae.

Winteraceae have long attracted students of angiosperm evolution and biogeography because of their putatively primitive morphology and disjunct Southern Hemisphere distribution (Australasia, South America, Madagascar). Emphasizing their vesselless wood and plicate (conduplicate) carpels, Thorne (1974) considered Winteraceae the most primitive living angiosperm family. Others (Walker & Walker, 1984; Cronquist, 1988; Takhtajan, 1997) argued that Magnoliales such as *Degeneria* are more primitive: although these have vessels, they also have plicate carpels, plus gymnosperm-like monosulcate pollen with a continuous tectum and granular infratectal structure, whereas Winteraceae have putatively more advanced pollen shed in permanent tetrads, with a round distal pore (ulcus), coarsely reticulate sculpture, and columellar infratectal structure. After concluding that angiosperms arose in the area of Southeast Asia and Australasia (cf. Takhtajan, 1969), Smith (1973) postulated that Winteraceae originated in Malesia and migrated south through Australasia and Antarctica to South America and west to Madagascar. This scenario was challenged by the theory of plate tectonics and rec-

ognition that Southeast Asia and Australasia are juxtaposed portions of two supercontinents, Laurasia and Gondwana, which were widely separated during the rise of angiosperms in the Early Cretaceous. Since only two species of Winteraceae occur outside the former limits of Gondwana (*Drimys granadensis* L. f. in Central America, *Tasmania piperita* (Hook. f.) Miers in the Philippines), which could be "spillovers" after South America and Australasia collided with Laurasia in the Tertiary, Winteraceae were soon offered as one of the best examples of a taxon with a Gondwanan distribution (Schuster, 1972, 1976; Raven & Axelrod, 1974).

Paleobotanical discoveries and phylogenetic analyses of the past two decades have shed new light on the history of Winteraceae and other angiosperm taxa. The purpose of this paper is to review the fossil record of Winteraceae in the context of the phylogenetic results, and thus to present an updated synthesis of the evolutionary and geographic history of the family, as background for discussion of *Takhtajania*. Of special interest is fossil pollen evidence extending the winteraceous line into the Early Cretaceous, which indicates that

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Winteraceae originated in more tropical environments than they inhabit today.

PHYLOGENETIC CONTEXT

Phylogenetic analyses have confirmed the position of Winteraceae among magnoliids, now recognized as a basal paraphyletic grade of angiosperms below monocots and eudicots (the 95% of dicots with tricolpate and derived pollen). However, they call into question the primitive status of vesselless wood, at least in Winteraceae.

Based on a morphological cladistic analysis of primitive angiosperms, Young (1981) concluded that Winteraceae and other vesselless taxa are nested well within the angiosperms, so it is more parsimonious to assume that vessels arose in the common ancestor of angiosperms and were lost in the vesselless taxa. This was confirmed by the analysis of Donoghue and Doyle (1989), which placed Magnoliales in a restricted sense, with granular exine structure, at the base of the angiosperms, with the remaining groups (including Winteraceae) united by columellar structure. Winteraceae were linked with Illiciales (*Illicium*, Schisandraceae) and in some trees Canellaceae, based on palisade exotesta, a similarity of Winteraceae, Illiciales, and Canellaceae noted by Corner (1976). Winteraceae and Illiciales had also been associated by Walker (1976), based in part on their coarsely reticulate pollen sculpture, and were subsequently linked in the morphological cladistic analysis of Loconte and Stevenson (1991). Another similarity of Winteraceae and Canellaceae is their irregular, "first rank" leaf venation (Hickey, 1977), with secondary veins that are poorly differentiated from higher vein orders and loop repeatedly inside the margin (Hickey & Wolfe, 1975). However, this may be a symplesiomorphy rather than evidence for direct relationship; similar venation occurs in Early Cretaceous angiosperm leaves and has been considered primitive (Wolfe et al., 1975; Doyle & Hickey, 1976; Hickey, 1977).

Since vessels are often viewed as unambiguously advantageous in allowing more efficient conduction, these cladistic results stimulated debate on the functional plausibility of loss vs. multiple origins of vessels. Donoghue and Doyle (1989) argued that loss might be less deleterious than assumed, since vesselless wood would be derived from wood with very primitive vessels, not advanced ones. Winteraceae and other vesselless angiosperms usually occur in cool, wet habitats; Carlquist (1975) argued that this is the only environment where they can persist, but Donoghue and Doyle (1989) noted that

it might also be the environment where loss of vessels would be least disadvantageous. Donoghue and Doyle and Feild et al. (2000) suggested that vessel loss might even be advantageous in cool climates, since embolisms caused by freezing would be restricted to one tracheid rather than expanding to fill a whole vessel. This is especially plausible for Trochodendrales (nested among lower eudicots with vessels: Chase et al., 1993; Hoot et al., 1999; Savolainen et al., 2000), which were common in the Late Cretaceous and Tertiary of northern Laurasia (Crane et al., 1991). Carlquist (1983, 1987, 1988, 1996) presented several arguments against the loss of vessels and for multiple origins: the parallel nature of advancement trends within vessels; the implausibility of scenarios for loss of vessels as a result of movement from dry to mesic (Young, 1981) or from aquatic to terrestrial habitats; the fact that vessels are almost but not completely lost in *Ephedra*, even in extreme habitats; and the lack of tracheid dimorphism in vesselless angiosperms. However, one argument of Bailey and Nast (1944) and Carlquist (1975), that the characteristic stomatal plugs of Winteraceae are a compensation for lack of vessels, appears to be incorrect. Feild et al. (1998, 2000) showed experimentally that plugs do not reduce transpiration and are more likely a device to promote runoff of water in cloud forest habitats.

Many aspects of earlier cladistic schemes now need revision as a result of molecular phylogenetic analyses. Studies of partial rRNA sequences (Hamby & Zimmer, 1992; Doyle et al., 1994) rooted angiosperms not in woody magnoliids but in "paleoherbs," with Nymphaeales basal, as did more recent morphological analyses (Doyle et al., 1994; Doyle, 1996). Much more extensive studies of *rbcL* (Chase et al., 1993) placed *Ceratophyllum* at the base of the angiosperms. However, this rooting was quickly suspected to be a long-branch effect (Qiu et al., 1993; Donoghue, 1994). This view has been confirmed by analyses of 18S rDNA (Soltis et al., 1997), cpITS (Goremykin et al., 1996; A. V. Troitsky, pers. comm. 1998), phytochrome genes (Mathews & Donoghue, 1999), and *atpB* (Savolainen et al., 2000), all of which root angiosperms among a series of taxa including not only Nymphaeales but also several woody magnoliid taxa: *Amborella*, *Austrobaileya*, Illiciales, and (based on studies of *rbcL* by Renner, 1999) Trimeniaceae. Significantly, these taxa occur together as a clade in *rbcL* trees (Chase et al., 1993). Endress (1987) and Donoghue and Doyle (1989) associated *Amborella* and Trimeniaceae with Chloranthaceae, but Chloranthaceae

now appear to be an isolated line, located above the basal grade.

All molecular analyses that have included the relevant taxa have separated Winteraceae from Illiciales and linked them with Canellaceae (Chase et al., 1993; Soltis et al., 1997; Mathews & Donoghue, 1999; Savolainen et al., 2000), making up a group that I will call Winterales. All genes except 18S (Soltis et al., 1997), for which the sampling of magnoliids was less complete, place Winterales in a clade with three other orders as defined by APG (1998): Laurales (Calycanthaceae, Monimiaceae s.l., *Gomortega*, Hernandiaceae, Lauraceae), Magnoliales (*Eupomatia*, Himantandraceae, *Degeneria*, Myristicaceae, Magnoliaceae, Annonaceae), and Piperales (Piperaceae, Saururaceae, Aristolochiaceae, *Lactoris*). Based on *rbcL* (Chase et al., 1993) and *rbcL* plus *atpB* (Savolainen et al., 2000), the sister group of Winterales is Magnoliales; based on phytochrome genes (Mathews & Donoghue, 1999) and *atpB* (Savolainen et al., 2000), their sister group is Piperales.

Like the morphological trees, the molecular trees imply that Winteraceae are secondarily vesselless, although interestingly they suggest that the absence of vessels in *Amborella* is primitive. They also call into question the view that the carpels of Winteraceae are primitive: the basal lines (*Amborella*, *Austrobaileya*, etc.) have ascidiate, not plicate carpels (Endress & Igersheim, 1997), implying that the plicate condition is derived. Igersheim and Endress (1997) also refuted statements that the carpels of Winteraceae and *Degeneria* are not completely closed (Bailey & Swamy, 1951; Eames, 1961); actually, their margins are postgenitally fused.

These molecular challenges to morphological cladistic results appear to be supported by preliminary analyses of an expanded morphological data set of magnoliids and basal monocots and eudicots (Doyle & Endress, in prep.), incorporating gynoeical data of Endress and Igersheim (1997, 1999) and Igersheim and Endress (1997, 1998). These analyses also move Illiciales near *Austrobaileya* and associate Winteraceae with Canellaceae, based on palisade exotesta and truncate stamen connective.

Phylogenetic analyses have also led to explicit hypotheses on relationships within Winteraceae. Vink (1988) presented two morphological trees of the family, which differed in rooting: one with *Tasmannia* basal, on the standard assumption that the ancestral chromosome number is $n = 13$ (as in *Tasmannia*) and $n = 43$ (as in other members) is derived; the other with *Takhtajania* basal, based on its elongate inflorescences, and *Tasmannia* and

Drimys linked as a clade, which he preferred. Because Vink assumed that *Takhtajania* has $n = 43$, based on its large pollen size (Pragowski, 1979), he suggested that $n = 13$ in *Tasmannia* is not ancestral but derived from $n = 43$. This poses a problem if the closest outgroup is Canellaceae, which have $n = 11, 13,$ and 14 (Kubitzki, 1993). In both trees, *Bubbia*, *Belliolum*, *Zygogynum*, and *Exospermum* formed a clade, linked with *Pseudowintera*. Two species of *Zygogynum* (*Z. balansae* Tiegh., *Z. pomiferum* Baill.) differ from the rest of the family in having monad pollen grains (Sampson, 1974); the position of *Zygogynum* within the family implies that these are secondarily derived from tetrads.

The first limited *rbcL* data (Chase et al., 1993) were more consistent with the first of Vink's (1988) trees in placing *Tasmannia* below *Drimys* and *Belliolum*, but they did not address the position of *Takhtajania*. Analyses of rDNA ITS sequences by Suh et al. (1993) showed unusually low divergence within Winteraceae, indicating either an implausibly recent age for the family or a slowdown in ITS evolution, and the presence of two ITS sequences in *Bubbia*, *Belliolum*, *Zygogynum*, and *Exospermum*, apparently reflecting an unusual persistence of polymorphism in ITS. Although unrooted, the tree obtained was consistent with the basal position of *Tasmannia* and the existence of a *Bubbia-Belliolum-Zygogynum-Exospermum* clade.

The rediscovery of *Takhtajania* has allowed placement of this genus and resolution of the apparent conflicts concerning chromosome number. Karol et al. (2000) included *Takhtajania* in analyses of ITS and *trnL-F* spacer sequences from Winteraceae and Canellaceae. Analyses of *trnL-F* indicated that either *Takhtajania* or *Tasmannia* could be basal in Winteraceae, but *Takhtajania* was basal in trees based on ITS and the two data sets combined. Other relationships within the family were the same as those found by Suh et al. (1993). These results are consistent with Vink's (1988) view that the inflorescences of *Takhtajania* are primitive. However, the finding that the chromosome number of *Takhtajania* may be $n = 18$ (Ehrendorfer & Lambrou, 2000) refutes his suggestion that $n = 13$ in *Tasmannia* is derived from $n = 43$, which does appear to be a synapomorphy of *Drimys* and the remaining groups.

FOSSIL RECORD

There are several old reports of fossil winteraceous leaves, but these were not based on a critical analysis of leaf architecture, and they have not

been reexamined recently. As noted above, Winteraceae have irregular “first rank” venation (Hickey, 1977), which has been considered primitive for angiosperms (Hickey & Wolfe, 1975), but otherwise their leaves are not very distinctive. Cuticle analysis might allow better evaluation of these determinations, for example by showing the stomatal plugs characteristic of most genera (Bailey & Nast, 1944; Feild et al., 1998).

Some leaf reports are from areas where Winteraceae occur today and winteroid pollen is known in the fossil record (cf. below). Berry (1938) described *Drimys patagonica* from the early Miocene of Argentina, said to resemble Winteraceae in having a “papillose” lower surface; the venation is consistent with Winteraceae, though probably not diagnostic. Dusén (1908) described *Drimys antarctica* from the Paleocene (Askin, 1992) of Seymour Island on the Antarctic Peninsula; the irregular spacing and angles of the secondary veins are consistent with Winteraceae. Deane (1902), miscited by Pragowski (1979) as Card (1902) and possibly the source of an unreferenced remark by Berry (1938), reported *Drimys* leaves from the Tertiary of New South Wales, but the fragment illustrated has no distinctive features. Leaves of Winteraceae have not been recognized in more recent studies of rich Australian Tertiary floras (Carpenter et al., 1994; Christophel, 1994; McLoughlin & Hill, 1996; R. S. Hill, pers. comm. 1999), which have used more critical methods of leaf identification.

More convincing is a report by Poole and Francis (2000) of vesselless wood described as *Winteroxylon jamesrossi* I. Poole & J. E. Francis from the mid-late Santonian–early Campanian of James Ross Island on the Antarctic Peninsula. Although the exact combination of pitting, ray, and parenchyma features does not occur any modern genus of Winteraceae, all are found within the family, and other vesselless angiosperm taxa (*Amborella*, Trochodendrales) are more different.

A few other megafossil reports are from outside the geographic range of modern Winteraceae and fossil records of winteroid pollen. Chaney and Sanborn (1933) described Oligocene leaves from Oregon as *Drimys americana* R. W. Chaney & Sanborn, but this is questionable, since the venation differs from that of Winteraceae in having thicker, more distinct secondary veins. Page (1979) compared vesselless wood from the Late Cretaceous (Maastrichtian) of California with Old World Winteraceae; she separated it from New World *Drimys* and Trochodendrales based on its abundant parenchyma. Gottwald (1992) described vesselless wood from the Eocene of Germany as *Winteroxylon mun-*

dlosi, which was similar enough to the Antarctic wood of Poole and Francis (2000) that they assigned their material to the same genus. If these fossils are winteraceous, they would imply that the family extended into Laurasia, as in Mexico and Malesia today. However, the possibility that they represent extinct vesselless lines not directly related to Winteraceae should also be considered, given the absence of more diagnostic winteroid pollen, the abundance of Trochodendrales in the Early Tertiary of Laurasia (Crane et al., 1991), and the presence of leaf cuticles with similarities to *Amborella* in the lower Potomac Group (Upchurch, 1984). Extinct vesselless lines should be more common if the lack of vessels in Winteraceae is primitive, since this would imply that the ancestors of many other taxa lower in angiosperm phylogeny were also vesselless.

The record of Winteraceae has been solidified and greatly extended by palynology, based on ulcerate tetrads closely comparable to the family (Figs. 1a, 2). Unlike the wood, the distinctive features of the pollen are clearly derived and thus more indicative of this particular clade. Winteroid tetrads are a persistent but minor element in latest Cretaceous and Tertiary rocks of Australasia (Dettmann & Jarzen, 1990), consistent with the low pollen production and subordinate ecological status of Winteraceae today. Such pollen was tentatively reported (without illustration) by Cranwell (1959) from the Paleocene of Seymour Island, and figured by Couper (1960) from the Oligocene of New Zealand as *Pseudowintera* sp. Couper’s material was named *Pseudowinterapollis* by Krutzsch (1970); similar tetrads from the latest Cretaceous through Miocene of southeastern Australia were named *Gephyrapollenites* (with three species) by Stover and Partridge (1973), who were apparently unaware of Krutzsch’s article. Martin (1978) indicated that the closest match for the Australian fossils is *Tasmaniania*. Mildenhall and Crosbie (1979) extended the range of *Pseudowinterapollis*, which they considered most similar to *Pseudowintera*, from the latest Cretaceous through the Pleistocene of New Zealand. As noted by Suh et al. (1993), since phylogenetic analyses indicate that *Pseudowintera* is nested within the family, these data imply that crown-group Winteraceae (i.e., the clade consisting of all derivatives of the most recent common ancestor of the living members: Doyle & Donoghue, 1993) originated before the end of the Cretaceous. These grains were accepted as Winteraceae by Muller (1981) in his critical review of pollen evidence for extant angiosperm families. In Australasia, the oldest record is from the mid-Campanian

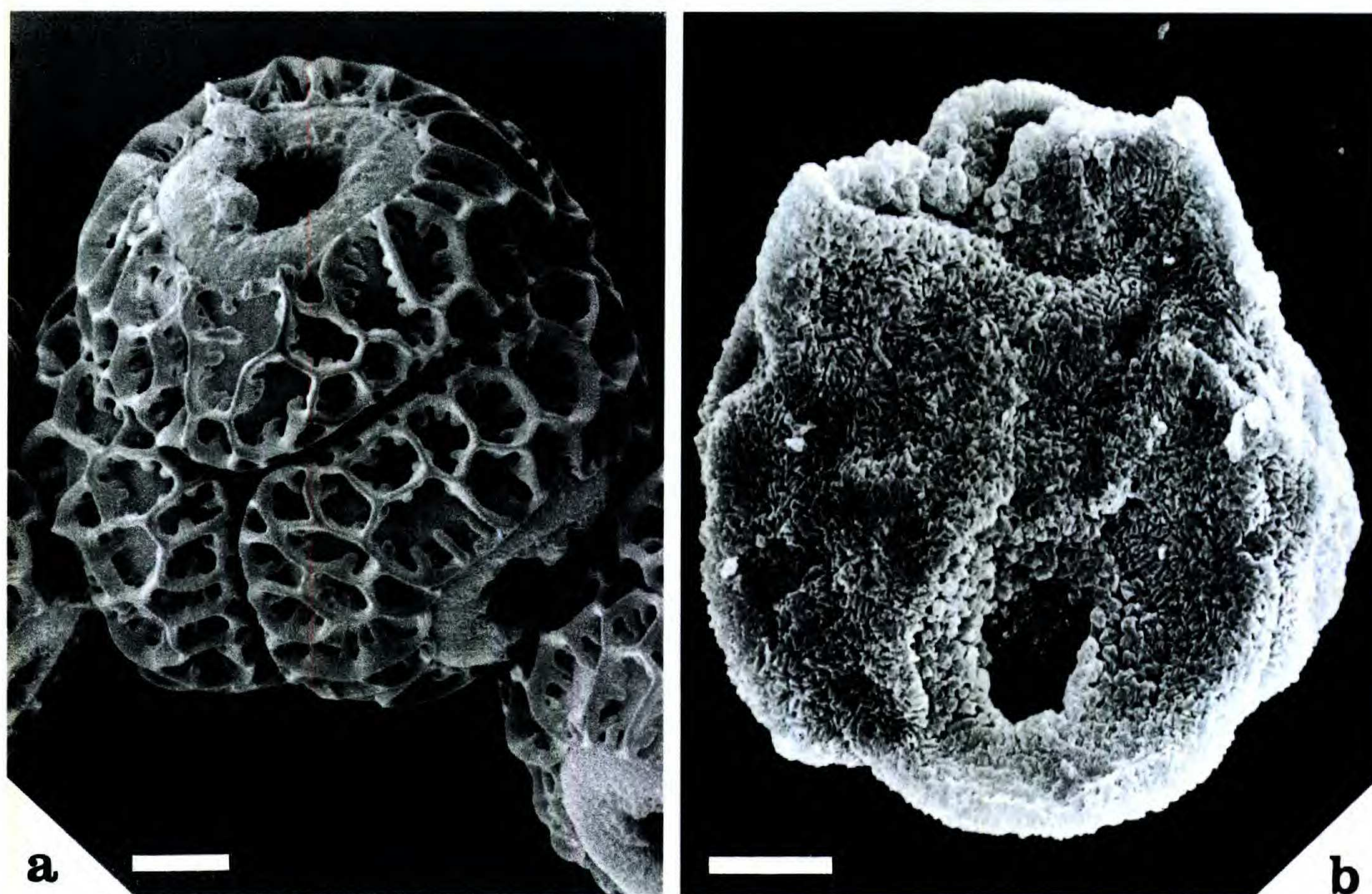


Figure 1. Recent and Early Cretaceous pollen tetrads, SEM. —a. *Drimys winteri* (cultivated, Davis, California). —b. *Walkeripollis gabonensis* (Doyle et al., 1990a), Zone C-VII (late Barremian?), Gabon. Scale bar = 5 μm .

of the Otway Basin of southeastern Australia (Dettmann & Jarzen, 1990). Winteraceae are also known from the Maastrichtian or Paleocene through the Miocene of central Australia (Twidale & Harris, 1977; Harris & Twidale, 1991; Macphail et al., 1994) and the Oligocene of Tasmania (Macphail & Hill, 1994). However, since the early report of Cranwell (1959), Winteraceae do not seem to have been observed in Tertiary pollen floras from Antarctica (Truswell & Drewry, 1984; Truswell, 1991; Askin, 1992).

Mildenhall and Crosbie (1979) also reported loose ulcerate tetrads and monads, named *Harrisipollenites*, from the Oligocene through Pleistocene of New Zealand, which they compared with the monads of *Zygogynum* species (Sampson, 1974). Since phylogenetic analyses indicate that monad-producing *Zygogynum* is one of the most apical branches in the family (Vink, 1988; Suh et al., 1993; Karol et al., 2000), this record is evidence that crown-group Winteraceae had diversified to a high level by the Oligocene. These considerations would further support the view of Suh et al. (1993) that the low divergence of ITS sequences within Winteraceae is due to a slowdown in molecular evolution, rather than a recent origin of the crown-group.

Two types of winteroid tetrads are also known

from Tertiary beds (considered early Miocene) of the Cape region in South Africa (Coetzee, 1981; Coetzee & Muller, 1984; Coetzee & Praglowski, 1988), where Winteraceae are now extinct. This implies that *Takhtajania* is the only survivor of a formerly more widely distributed assemblage of Winteraceae in the African-Madagascan region. The same floras contain other taxa that no longer occur in mainland Africa but persist in Madagascar: *Ascarina* (Chloranthaceae), *Casuarina*, Cupanieae (Sapindaceae), and Sarcolaenaceae. However, according to Coetzee and Muller (1984) and Coetzee and Praglowski (1988), these fossils are most similar not to pollen of *Takhtajania*, but rather to that of the Australasian genera *Tasmannia* ("*Drimys*" *piperita*) and *Bubbia* ("*Zygogynum*" *queenslandianum*).

Although pollen of *Drimys* occurs at low frequencies in the Quaternary of Chile (e.g., Heusser, 1981), there have been few reports of winteroid tetrads from older sediments in South America, although such rocks have been extensively studied (cf. Askin & Baldoni, 1998). Apparently the oldest are grains identified by Baldoni (1987) as *Gephyropollenites calathus* Partridge from the Paleocene-Eocene of Argentina. Barreda (1997) reported *Pseudowinteripollis couperi* Krutzsch from the Oligo-Miocene of Argentina; she provided SEM figures

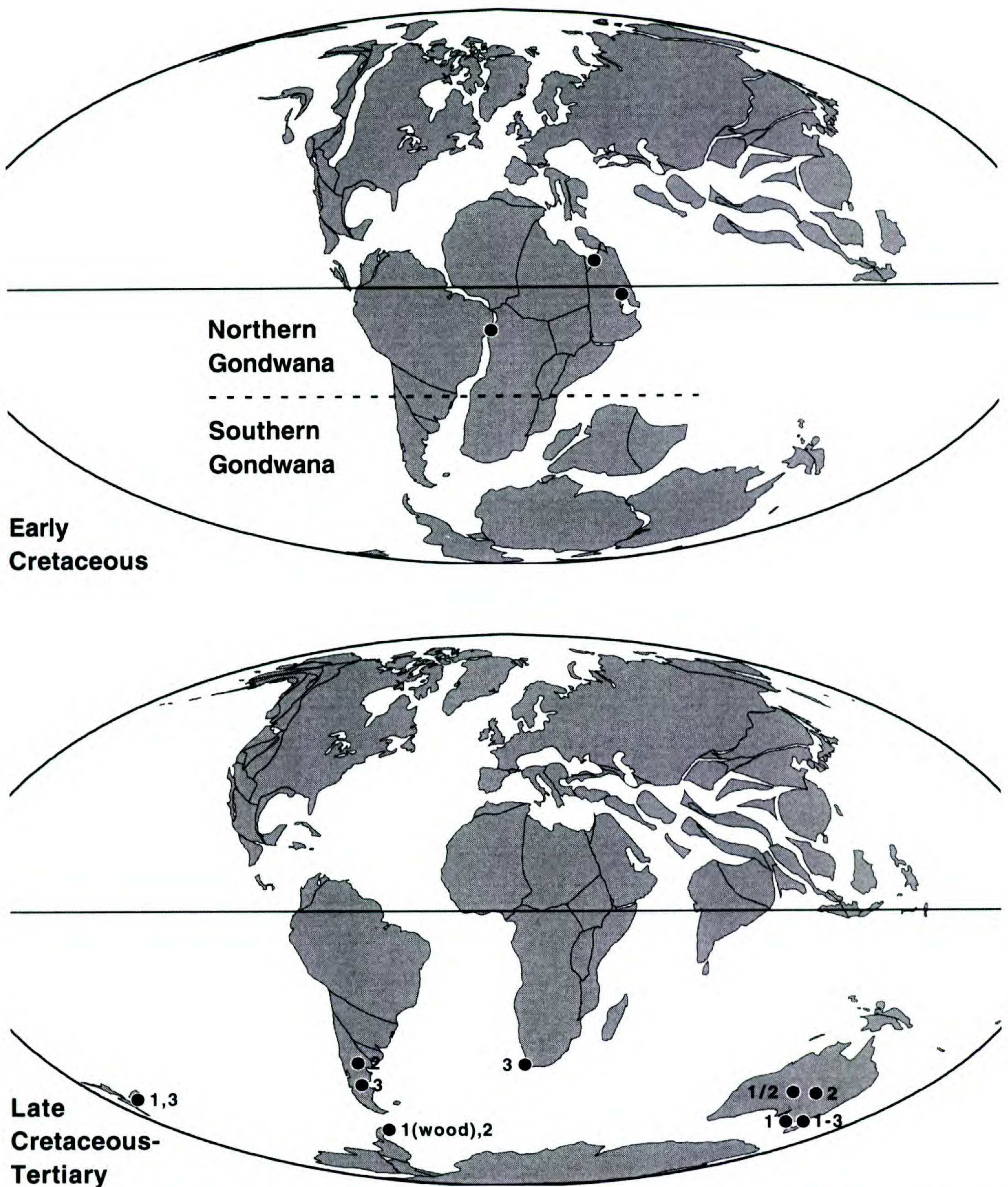


Figure 2. Pre-Quaternary occurrences of ulcerate tetrad pollen related to Winteraceae and vesselless wood of Poole and Francis (2000). Top, Early Cretaceous (base map 120 My, Barremian-Aptian: Scotese, 1997). Bottom, Late Cretaceous and Tertiary (base map 50 My, Eocene: Scotese, 1997); 1: Campanian, Maastrichtian; 2: Paleocene, Eocene; 3: Oligocene, Miocene, Pliocene. See text for references.

showing a tetrad closely comparable to *Drimys* in sculpture and presence of a well-defined annulus.

The stratigraphic and geographic range of winteroid pollen was extended dramatically by Walker et al. (1983), based on tetrads in two cores from the late Aptian-early Albian of Israel. At this time (Fig. 2), Israel was part of the Northern Gondwana

province of Brenner (1976), which straddled the Early Cretaceous equator and included all but the southern portions of Africa and South America. In contrast, Late Cretaceous, Tertiary, and Recent occurrences of Winteraceae (except those in Central America and Malesia) are in regions that belonged to Brenner's Southern Gondwana province in the

Early Cretaceous. The Israeli tetrads, designated *Walkeripollis* sp. A by Doyle et al. (1990a), resemble pollen of modern Winteraceae in having a round ulcus consisting of a central pore surrounded by a thicker annulus, underlain by a safranin-staining ring that Walker et al. (1983) assumed was thickened endexine, as in many modern Winteraceae (Pragowski, 1979). However, Walker et al. interpreted them as more primitive than living Winteraceae because of their finer, foveolate-reticulate sculpture.

Still older winteroid pollen was described by Doyle et al. (1990a, b) from the Cretaceous of Gabon, as *Walkeripollis gabonensis* J. A. Doyle, Hotton & J. V. Ward (Fig. 1b). These tetrads appear to be even more primitive in having a slightly elliptical aperture (presumably transitional from a sulcus) and foveolate sculpture, with small tectal perforations only. Transmission electron microscopy (TEM) confirmed that the endexine is thickened under the annulus. These grains were found in only one sample, from an interval (Zone C-VII) near the end of filling of the nascent South Atlantic rift with continental sediments, but they are fairly common in this sample. Their significance was overlooked by Doyle et al. (1977, 1982), who assumed that they were tetrad-producing variants of *Tucanopollis crisopolensis* (Regali, Uesugui & A. S. Santos) Regali, a common angiosperm in these beds, which also has a round, sculptured aperture. The age of Zone C-VII and its equivalents in Brazil was originally considered early Aptian (Doyle et al., 1977, 1982), but Regali and Viana (1989) and Doyle (1992) argued that it is late Barremian, based in part on reports of two associated new groups, *Afropollis* and tricolpate pollen, in independently dated late Barremian rocks in Morocco (Gübeli et al., 1984) and England (Penny, 1989) (and more recently Israel: P. J. De Haan, unpublished Ph.D. thesis, Botany, Univ. California, Davis, 1997).

Compared with modern Winteraceae, both *Walkeripollis gabonensis* and *W.* sp. A are anomalous in being calymmate (Van Campo & Guinet, 1961), with the tectum partially continuous between adjacent monads of the tetrad. In this respect, they appear more advanced than the acalymmate tetrads of the modern taxa, where the tectum stops at the junction between monads. Since the circular aperture and coarser reticulum of *Walkeripollis* sp. A suggest that this species is phylogenetically closer to modern Winteraceae than *W. gabonensis*, Doyle et al. (1990b) inferred that the calymmate condition arose in the common ancestor of the two species and reversed to acalymmate in modern Winteraceae, along with coarsening of sculpture. The fact

that *Walkeripollis* is calymmate may be grounds for caution in relating it to Winteraceae, but *W.* sp. A is almost perfectly intermediate between *W. gabonensis* and modern Winteraceae, and both species are only weakly calymmate, implying that the reversal required would be minor. The fact that both *Walkeripollis* species have a conspicuous annulus, like *Takhtajania*, *Drimys*, *Belliolum*, and *Zygogynum* species with monads (Pragowski, 1979), suggests that the lack of a well-differentiated annulus in *Tasmannia*, *Pseudowintera*, *Bubbia*, *Exospermum*, and *Zygogynum* species with tetrads is derived. Absence of an annulus seems loosely correlated with smaller aperture size. *Exospermum* and *Zygogynum* are most like *Walkeripollis* in having fine sculpture, but their position in morphological and molecular phylogenies (Vink, 1988; Suh et al., 1993; Karol et al., 2000) implies that this condition is secondarily derived.

Winteroid tetrads may be more widespread in the Early Cretaceous than reported so far. In the middle Albian Khafji member of the Wasia Formation of offshore Saudi Arabia, S. L. Gaponoff (pers. comm. 1990 & 1999) found a single tetrad, which is similar to *Walkeripollis* sp. A in sculpture but looser and apparently acalymmate, suggesting that it is still more closely related to crown-group Winteraceae. But so far there is a gap in the record of such pollen through the first half of the Late Cretaceous.

A possibly related pollen group consists of foveolate-reticulate, ulcerate monads from the early Aptian to Albian of Israel, described by Brenner and Bickoff (1992) as *Retimonoporites operculatus* G. J. Brenner & Bickoff. Their sculpture is roughly similar to that of *Walkeripollis* sp. A; the ulcus is covered by an operculum and underlain by a dark-staining area interpreted as endexine. Because these monads predate *W.* sp. A in Israel, Brenner (1996) interpreted them as representing a more primitive, pre-tetrad state; however, they are probably younger than *W. gabonensis*. It is possible that these grains are related to Winteraceae, but there are enough differences to make this view somewhat speculative. They are much smaller than the monads of *Walkeripollis*, the ulcus is proportionally smaller, and the endexine forms a solid patch rather than a ring around the border of the ulcus.

Doyle et al. (1990a, b) also suggested that two other Cretaceous pollen groups may be related to Winteraceae: *Afropollis*, which is abundant from the late Barremian through the early Cenomanian of Northern Gondwana, and *Schrankipollis*, from the Aptian of Egypt and Maryland. *Afropollis* varies from operculate or zonosulculate in the oldest species to inaperturate in younger ones, with a loose

reticulum surrounding a central body, and the operculates have typical angiospermous columellae below the reticulum. *Schrankipollis* is zonosulcate but elliptical and more finely sculptured. The comparison with Winteraceae was based primarily on the fact that *Afropollis*, *Schrankipollis*, and *Walkeripollis gabonensis* all have finely segmented muri and tend toward circular shape and a round aperture, with the zonosulcus presumably derived by broadening of an operculum. Based on a cladistic analysis of these fossils and pollen of living Winteraceae and Illiciales, Doyle et al. (1990b) inferred that *Afropollis* and *Schrankipollis* belong to an extinct sister group of *Walkeripollis*, Winteraceae, and Illiciales. The two *Walkeripollis* species were successive branches of the stem-lineage leading to both Winteraceae and Illiciales, based on the elliptical aperture of *W. gabonensis* and the finer sculpture of both species. The trichotomosulcate (“syntricolpate”) monads of Illiciales were linked with modern winteraceous tetrads by their coarse sculpture, implying that they are secondarily derived from tetrads. Because this analysis placed *Walkeripollis* on the stem-lineage to Winteraceae and Illiciales, and Illiciales have vessels, Doyle et al. (1990b) speculated that the plants producing *Walkeripollis* still had vessels.

This scheme can no longer be defended, since only the tetrads seem securely related to Winteraceae, and molecular evidence against a relationship of Illiciales and Winteraceae has become overwhelming (cf. above). Doyle et al. (1990a, b) acknowledged that the winteraceous affinity of *Afropollis* and *Schrankipollis* was more speculative. They noted that *Afropollis* is anomalous in having a thick endexine all around the grain, as in gymnospermous seed plants, rather than under the aperture only, as in Winteraceae and most other magnoliid angiosperms. Because other characters of *Afropollis* seemed so angiospermous, and because a few magnoliids do have a thick endexine, they suggested that the endexine character may not rule out angiosperm affinities. However, Friis et al. (1999) have found *Afropollis* in separate pollen sacs with no evident angiosperm features. A similar combination of gymnospermous endexine and angiospermous columellae and sculpture also occurs in the Late Triassic Crinopolles pollen group, which Cornet (1989) interpreted as angiospermous, but which Doyle and Hotton (1991) and Doyle and Donoghue (1993) suggested is related to the angiosperm crown-group but more primitive—i.e., on the angiosperm stem-lineage. By the same reasoning, *Afropollis* might also be a side-line of the angiosperm stem-lineage that persisted into the Cretaceous.

These doubts do not apply to *Schrankipollis*, since it has only a little endexine under the aperture, but without *Afropollis* to link it with Winteraceae, there is little reason to associate it with the family.

Scenarios for origin of the tetrad pollen of Winteraceae also need revision in light of molecular and morphological evidence that Canellaceae are the sister group of the family. Pollen of Canellaceae is small, round, and monosulcate, with occasional trichotomosulcate variants (Wilson, 1964; Walker, 1976; J.-M. Groult, unpublished D.E.A. thesis, Muséum National d'Histoire Naturelle, Paris, 1998). Its exine structure varies from granular with a continuous scabrate tectum (*Capsicodendron*) to columellar and either foveolate (most genera) or reticulate (*Cinnamosma*). Walker (1976) assumed that the granular extreme is primitive, as part of a general trend in angiosperms as a whole. This would imply that columellae arose independently in Canellaceae and Winteraceae. The idea that granular structure is primitive in angiosperms was supported by the analysis of Donoghue and Doyle (1989), which placed Magnoliales at the base of the angiosperms, but in more recent analyses, where Magnoliales are nested within woody magnoliids, their granular structure is a reversal. Canellaceae are rooted differently in trees based on ITS and *trnL-F* (Karol et al., 2000), but the unrooted tree is the same, and *Capsicodendron* is not basal in either tree. This suggests that the common ancestor of Winteraceae and Canellaceae had small, round, monosulcate pollen with columellae and foveolate sculpture, a type common in the Early Cretaceous. Such pollen may go back to the first angiosperms; for example, it occurs in the near-basal genus *Austrobaileya* (Endress & Honegger, 1980). These data also remove the basis for the conjecture that the parent plants of *Walkeripollis* had vessels (Doyle et al., 1990b). Based on pollen morphology, a phylogenetic analysis would place Canellaceae below *Walkeripollis*, so vessels could have been lost at any point on the line leading to crown-group Winteraceae, either before or after *Walkeripollis*.

GEOGRAPHIC HISTORY AND ECOLOGICAL EVOLUTION

Fossil data suggest that the stem-lineage leading to Winteraceae, represented by *Walkeripollis*, originated in the tropical zone of Northern Gondwana. This is consistent with the view of Raven and Axelrod (1974) that angiosperms as a whole originated in this region. The Early Cretaceous climate in the classic areas of Gabon and Brazil has been interpreted as hot and dry (Brenner, 1976; Doyle et al.,

1977, 1982), based on the low frequency of spores, abundance of *Classopollis* (the conifer family Cheirolepidiaceae, noted for its xeromorphic vegetative morphology) and ephedroid pollen (related to modern Gnetales, of which *Ephedra* and *Welwitschia* are desert plants), and the presence of thick Aptian salt deposits, which mark the first influx of marine water into the rift. However, there is evidence for wetter conditions in the Middle East and northern South America, which were near the equator rather than about 15 degrees to the south: less common *Classopollis* and ephedroids, abundant fern spores and Araucariaceae, and occasional coals (Doyle et al., 1982; McCabe & Parrish, 1992; Brenner, 1996). Interestingly, *Walkeripollis* occurs in both areas, suggesting that its parent plants could tolerate some range of rainfall. The fact that *W. gabonensis* is from a rift sequence raises the possibility that its parent plants were growing in cooler upland areas flanking the rift. However, models for rift evolution predict that relief would decrease with time, and although the presence of bisaccate podocarpaceous pollen suggests that there were high elevations near the rift in the earliest Cretaceous, such pollen had disappeared by the time *Walkeripollis* appeared in the Barremian (Doyle et al., 1982).

This scenario also fits the present distribution of probable outgroups of Winteraceae. Canellaceae are entirely African, Madagascan, and American, and Walker (1971) and Raven and Axelrod (1974) interpreted them as of Northern Gondwanan origin. Ecologically, they are more tropical than Winteraceae, and they extend into drier environments (Kubitzki, 1993). The second outgroup to Winteraceae, whether Magnoliales or Piperales, is less well established. However, if Magnoliales are the second outgroup, it may be significant that *rbcL*, *atpB*, and the two genes combined indicate that the basal branch in this group is Myristicaceae (Chase et al., 1993; Savolainen et al., 2000), which have a geographic distribution that also suggests a Northern Gondwanan origin (Walker, 1971; Raven & Axelrod, 1974). Myristicaceae are also a lowland tropical group, and although their species diversity is highest in Asia, Walker and Walker (1981) argued that their most primitive members are the Madagascan genera *Mauloutchia* and *Brochoneura*, which have helical rather than whorled stamens (a view confirmed by a morphological cladistic analysis by H. Sauquet, unpublished D.E.A. thesis, Univ. Pierre et Marie Curie, Paris, 1999).

Thus both fossil distributions and phylogenetic results suggest that the temperate, Southern Gondwana distribution of crown-group Winteraceae came about by southward migration and radiation

of plants derived from a stem-lineage in the lowland tropics. In the Early Cretaceous, Southern Gondwana was characterized by Podocarpaceae, Araucariaceae, and abundant spore-bearing plants (Brenner, 1976; Herengreen et al., 1982; Dettmann, 1994), suggesting cool, wet conditions like those where Winteraceae grow today. These data may fit the hypothesis discussed above that vessels were lost in cool, wet environments because of their susceptibility to embolisms caused by freezing (Donoghue & Doyle, 1989; Feild et al., 2000).

A major unresolved problem is when exactly Winteraceae moved into the temperate zone, and by what route. After the records of *Walkeripollis* in the Early Cretaceous, the line is not known until the Santonian-Campanian of Antarctica, represented by *Winteroxylon* wood (Poole & Francis, 2000), and the Campanian-Maastrichtian of Australia and New Zealand (Stover & Partridge, 1973; Mildenhall & Crosbie, 1979; Dettmann & Jarzen, 1990), represented by coarsely reticulate tetrads resembling crown-group Winteraceae. These tetrads seem well established in Australasia, and there are no records of them in the tropics (although given the rarity of earlier reports the significance of such negative evidence can be questioned). Migration to Southern Gondwana would pose little problem in the Early Cretaceous, when the continents were still largely connected (Fig. 2). However, by the time the crown-group is first recognized, ocean barriers had become much wider, especially between Northern Gondwana and Australasia. Possible scenarios may be considered in terms of continental positions ca. 6 My before the Campanian (Fig. 3; Scotese, 1997).

One route to Australasia might be through South America and Antarctica, which was attached to Australia until late in the Cretaceous. On paleogeographic grounds, it is more likely than not that the stem-lineage occurred in South America. In the Early Cretaceous, Brazil and Gabon were two sides of the same rift valley, and given the rarity of *Walkeripollis*, the lack of reports from Brazil is probably not significant. However, if the crown-group spread from South America to Australasia in the Late Cretaceous, it would also have to disperse across the South Atlantic in one direction or the other to explain its Tertiary and Recent occurrences in Africa (Coetzee & Muller, 1984) and Madagascar (*Takhtajania*). This scenario implies that near-basal lines of Winteraceae occurred in South America in the Late Cretaceous, which may conflict with the relatively nested position of the American genus *Drimys* in the family and the rarity of reports of pre-Quaternary winteroid pollen in South America

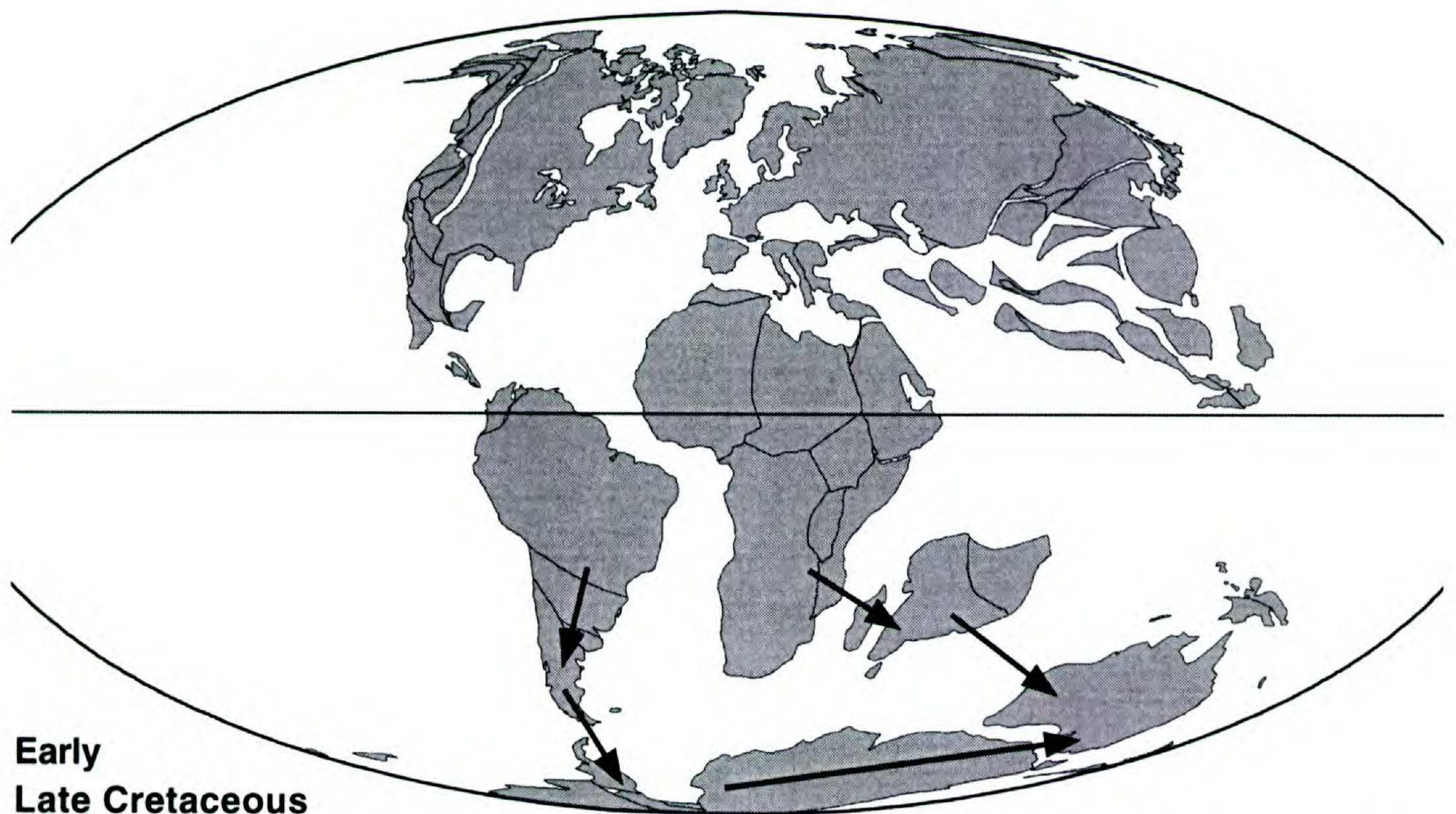


Figure 3. Paleogeography near the time of inferred dispersal of crown-group Winteraceae from Northern Gondwana to Australasia (90 My, Turonian: Scotese, 1997), showing alternative routes through South America-Antarctica and Madagascar-India.

(despite numerous palynological studies: cf. Askin & Baldoni, 1998), as compared with Australasia.

Another route to Australasia might be through Madagascar. Gondwana began to split into East Gondwana (Madagascar, India, Antarctica, Australasia) and West Gondwana (Africa, South America) in the Middle Jurassic (Rabinowitz et al., 1983). However, for some time Madagascar and India, which belonged to the Southern Gondwana province in the Early Cretaceous (Brenner, 1976; Hengreen et al., 1982; Dettmann, 1994), formed a block that might have acted as a stepping stone between Africa and Australasia and/or Antarctica (Fig. 3). This scenario might fit molecular evidence that *Takhtajania* is basal in Winteraceae (Karol et al., 2000): *Takhtajania* would represent a branch that stayed near the original Northern Gondwana area, while the rest of the family was derived from a branch that dispersed to Australasia. *Drimys* could be a line that dispersed later from Australasia to South America via Antarctica (Raven & Axelrod, 1974), consistent with its position in the family.

If, however, Winteraceae in the Tertiary of South Africa were related to modern Australasian genera (Coetzee & Muller, 1984; Coetzee & Praglowski, 1988), more complex scenarios must be envisioned, with a wider Cretaceous distribution of the crown-group and many local extinctions. The discovery of winteraceous wood in the Late Cretaceous of Antarctica (Poole & Francis, 2000) also suggests it

would be premature to favor one scenario over another: it implies that Winteraceae reached Antarctica very early, from which they could easily spread to either Australasia or South America. Better evidence on the phylogenetic position of known Cretaceous and Tertiary fossils, or discoveries of new fossils, could greatly clarify the geographic history of the family.

CONCLUSIONS

The stem-lineage leading to Winteraceae is one of the oldest recognizable angiosperm lines, extending back to the Barremian stage of the Early Cretaceous in Northern Gondwana. Modern Winteraceae appear to be derived from a line that spread from the tropics into the southern temperate zone, where Winteraceae were widespread in the latest Cretaceous and Tertiary, but the details are uncertain. Major priorities are to fill in the Late Cretaceous record and to clarify the time of appearance of crown-group Winteraceae in Africa-Madagascar, Antarctica, and South America. Hopefully this paper will alert palynologists and paleobotanists working in the Gondwana continents to winteraceous pollen and megafossils, and thus contribute to a more detailed reconstruction of the history of this important family of primitive angiosperms.

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